

NATURAL HYBRIDIZATION IN *TILLANDSIA* SUBGENUS *TILLANDSIA*

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BACKGROUND

Tillandsia L. subgen. *Tillandsia* (Bromeliaceae) are primarily epiphytic monocots and are distributed over much of the New World tropics and subtropics. They have dispersed into a wide range of habitats and exhibit a tremendous diversity in characteristics of the plant body, inflorescence and flower. Many distinctions are apparently related to habitat selection, although several species of the same subgenus often occur sympatrically (Benzing, 1981). Closely related sympatric species often differ greatly in vegetative characters. Some differences may be related to niche adaptation. Other species more likely result from differences in genetic backgrounds which limit the way a given species can adapt to a particular environment.

Morphological and physiological adaptations have allowed tillandsioid species to occupy various epiphytic and saxicolous niches (Benzing, 1980). An efficient means of seed dispersal, by wind, has allowed *Tillandsia* to reach many new places. This vagility and adaptability to a wide variety of hosts and climates have resulted in a mosaic of morphological forms. Determination of relationships among these taxa has been a great challenge to taxonomists who have worked with the group (Smith and Downs, 1977).

Natural hybridization appear to be responsible for some portion of the phenetic variations expressed by these species. Evidence for its occurrence has previously been reported (Smith and Downs, 1977; The Bromeliad Society, Inc., 1977). Fourteen interspecific hybrids are reported by Smith and Downs, including artificial crosses and putative natural hybrids. Five of these involved species of subgen. *Tillandsia*. The Bromeliad Society, Inc. listed 14 artificial and interspecific hybrids of *Tillandsia* subgen. *Tillandsia* (Table 1). Four were bigeneric crosses involving *Vriesea*. Six putative natural hybrids between members of subgen. *Tillandsia* are among the living collections of Werner Rauh at the University of Heidelberg's Botanical Gardens (Table 2). Additional evidence that natural interspecific hybridization occurs among species of *Tillandsia* subgen. *Tillandsia* has been accumulated. Its occurrence appears to be more widespread than has previously been recognized.

Ample opportunity exists for hybridization among species of subgen. *Tillandsia* as several species often occupy the same host and flower simultaneously. For example in the thorn forest of coastal Tamaulipas in northern Mexico, *T. polystachia* L., *T. paucifolia* J. G. Baker, *T. balbisiana* Schultes, *T. fasciculata* Swartz, *T. ionantha* Planchon, *T. schiedeana* Steudel, *T. baileyi* Rose, and *T. utriculata* L. grow in a dense, mixed community. Flowering seasons overlap and putative hybrids were collected.

A slight difference in flowering seasons is not an effective barrier to crossing because of the extended period over which flowers are usually produced. Each flower typically lasts approximately two days without closing during the night. Diurnal phenology along, therefore, is not a strong barrier between nocturnal and diurnal species. Other factors, e.g., pollinator attraction or postpollination isolation mechanisms, are apparently more important. Length of the corolla tube could provide a barrier between some species when the same animal visits both. However, the slight variation in corolla length among some sympatric species suggests other mechanisms are more

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Table 1

Tillandsia hybrids listed in the International Checklist of Bromeliad Hybrids involving members of the subgenus *Tillandsia*.

<i>Tillandsia brachycaulos</i> × <i>T. bulbosa</i>
<i>Tillandsia brachycaulos</i> × <i>T. caput-medusae</i>
<i>Tillandsia brachycaulos</i> × <i>T. ionantha</i>
<i>Tillandsia brachycaulos</i> × <i>T. streptophylla</i>
<i>Tillandsia fasciculata</i> × <i>T. foliosa</i>
<i>Tillandsia fasciculata</i> × <i>T. lieboldiana</i>
<i>Tillandsia fasciculata</i> × <i>Vriesea</i> 'Souv. de Joseph Mawet'
<i>Tillandsia flabellata</i> × <i>V. incurvata</i>
<i>Tillandsia flabellata</i> × <i>T. tricolor</i>
<i>Tillandsia heterophylla</i> × <i>T. multicaulis</i>
<i>Tillandsia imperialis</i> × <i>V. 'Baron de Selys'</i>
<i>Tillandsia ionantha</i> × <i>T. schiedeana</i>
<i>Tillandsia lindenii</i> × <i>T. tricolor</i>
<i>Tillandsia multicaulis</i> × <i>V. 'Mariae'</i>

Table 2

Natural hybrids of *Tillandsia* in the living collection of the University of Heidelberg Botanical Gardens, collected and determined by Werner Rauh.

<i>Tillandsia brachycaulos</i> × <i>T. caput-medusae</i>	Rauh 30431A & 45939
<i>Tillandsia brachycaulos</i> × <i>T. balbisiana</i>	Rauh 52374
<i>Tillandsia brachycaulos</i> × <i>T. capitata</i>	Rauh 52368
<i>Tillandsia brachycaulos</i> × <i>T. seleriana</i>	Rauh 44165 & 44163
<i>Tillandsia brachycaulos</i> × <i>T. valenzuelana</i>	Rauh 44164
<i>Tillandsia caput-medusae</i> ×	Rauh 45939

important. Some variation among sympatric species in microclimate preference has been noted, e.g., in Tamaulipas, Mexico, *T. baileyi* generally occurs in denser shade than do sympatric *T. paucifolia*, *T. balbisiana*, or *T. schiedeana*. This distinction does not seem to be sufficient to discourage promiscuous pollination visitations.

Evidence of hybridization is principally morphological. Scatter diagrams are a convenient method of illustrating the distribution of attribute pairs in a hybrid population. Principal component analysis (PCA) is a method of data reduction that has proven useful for analyzing hybridity (Wiley, 1981). Examination of pollen fertility is another method of determining hybridity (Wilson, 1980).

METHODS

The NT-SYS computer programs of Rohlf et al. (1980) were used to do PCA. The result of this procedure was used to construct three-dimensional diagrams graphically illustrating the phenetic relationships among putative parental and hybrid specimens. The characters used are listed in Appendices 1 & 2. Scatter diagrams were used to illustrate the distribution of character state pairs in one putative hybrid population.

Pollen samples from fresh, dried or alcohol-preserved flowers were stained with lactophenol-cotton blue (Wilson, 1980). A minimum of 200

grains was counted for each sample. Pollen fertility was estimated by calculating the number of stained versus the total stained and unstained pollen grains. Pollen viability estimates are reported for 50 species plus five putative hybrids and from two or more plants each of five species or putative hybrid populations. Three of these were duplicates from the same population. The other two, *T. fasciculata* and *T. capitata* Grisebach, are species that vary greatly among populations. Smith and Downs (1977) recognized 10 varieties of the former and two in the latter.

Voucher specimens are deposited at SEL.

RESULTS

Forty-six of the pollen samples tested were estimated to be more than 90% fertile; seven more were between 80% and 90%. Two species, not suspected of being hybrids or introgressants, had pollen viability of only 50% to 60%, another had less than 10%. Individuals, suspected of being hybrids, had from zero to 50% pollen viabilities. Pollen viability estimates are presented in Table 3.

Table 3

Pollen viability estimates for some *Tillandsia* species and putative hybrids.

Source of pollen: F - fresh flowers, A - flowers preserved in alcohol, D - dried specimens. NOTE: flowers in alcohol represent a population sample and may include pollen from several individuals.

Species	Source	Percentage viability	Collection number
<i>acostae</i>	A	94.6	Gardner 1023
<i>aguascalientensis</i>	A	94.6	Gardner 1322
<i>albida</i>	A	98.5	Gardner 331
<i>argentea</i>	A	100.0	Gardner 1099
<i>baileyi</i>	A	99.0	Gardner 1165
<i>bartramii</i>	D	98.7	Luther s.n.
<i>bourgaei</i>	A	99.0	Gardner 1139
<i>butzii</i>	A	67.2	Gardner 1100
<i>califanii</i>	A	96.1	Gardner 1293
<i>capitata</i>	F	89.4	Gardner 1429
<i>capitata</i>	F	96.9	Gardner 1459
<i>capitata</i>	F	94.8	Ariza-Julia s.n.
<i>caput-medusae</i>	A	97.3	Gardner 1120
<i>caput-medusae</i> × <i>brachycaulos</i>	F	15.5	Meilleur s.n.
<i>carlsoniae</i>	A	95.8	Gardner 1092
<i>chaetophylla</i>	A	98.2	Gardner 1378
<i>chiapensis</i>	A	84.6	Gardner 1111
<i>chlorophylla</i>	A	99.6	Gardner 1027.5
<i>circinnatoides</i>	A	96.7	Gardner 1138
<i>compressa</i>	A	95.1	Gardner 1117
<i>compressa</i> × <i>fasciculata</i>	F	39.5	Gardner 1117.5
<i>concolor</i>	D	97.9	Gardner 1288
<i>dugesii</i>	F	93.0	Gardner 1317

<i>ehrenbergii</i>	A	91.9	Gardner 1321
<i>eizii</i>	D	96.3	Gardner 1409
<i>erubescens</i>	A	07.6	Gardner 889
<i>fasciculata</i> var. <i>densispica</i>	D	90.1	Gardner 1175
<i>fasciculata</i>	F	87.7	Gardner 901
<i>festucoides</i>	D	93.6	Gardner 1124
<i>filifolia</i>	A	98.5	Gardner 1155
<i>flabellata</i>	D	94.1	Gardner 1426
<i>hubertiana</i>	D	37.5	Gardner 212.9
<i>imperialis</i>	A	98.5	Gardner 1292
<i>ionantha</i>	A	92.5	Gardner 922
<i>jalisco monticola</i>	A	97.0	Gardner 1350
<i>jalisco monticola</i>	F	52.6	Gardner 1445
<i>jalisco monticola</i>	F	93.4	Gardner 1445
<i>jalisco monticola</i> × <i>xerographica</i>	F	21.9	Gardner 1448
<i>karwinskyana</i>	A	85.7	Gardner 816
<i>kirchoffiana</i>	A	99.3	Gardner 880
<i>lampropoda</i>	A	96.0	Gardner 1076
<i>langlasseana</i>	F	93.4	Gardner 1506
<i>limbata</i>	A	81.4	Gardner 835
<i>limbata</i>	D	98.7	Gardner 1002
<i>oaxacana</i>	D	96.7	Gardner 1264
× <i>polita</i>	F	00.0	Gardner 1085
× <i>polita</i>	F	00.0	Gardner 1085
× <i>polita</i>	F	04.0	Gardner 1085
× <i>polita</i>	F	00.3	Gardner 1085
× <i>polita</i>	F	02.2	Gardner 1085
× <i>polita</i>	D	17.7	Gardner 1085
<i>ponderosa</i>	A	98.4	Gardner 1103
<i>prodigiosa</i>	A	97.5	Gardner 1264.1
<i>pseudobaileyi</i>	A	66.2	Gardner 1118
<i>punctulata</i>	A	95.2	Gardner 879
<i>punctulata</i> × <i>kirchoffiana</i>	A	50.3	Gardner 881
<i>rodrigueziana</i>	A	93.6	Gardner 1083
<i>rodrigueziana</i>	A	80.6	Gardner 1275
<i>roland-gosselinii</i>	A	94.4	Gardner 1214
<i>schiedeana</i>	A	91.1	Gardner 1121
<i>seleriana</i>	A	93.7	Gardner 1061
<i>streptophylla</i>	A	96.3	Gardner 1119
<i>utriculata</i> var. <i>utriculata</i>	A	92.5	Gardner 1007
<i>vicentina</i> var. <i>glabra</i>	A	97.5	Gardner 1091
<i>violacea</i>	A	97.0	Gardner 1462
<i>xerographica</i>	F	87.4	Gardner 1212

Observation of morphological variation within several populations of *Tillandsia* suggested that two basic types of hybridization occur: random hybridization and introgressive hybridization. In most cases of aberrant patterns of variation that were interpreted as due to interspecific hybridization a single

individual, or occasionally a few individuals, was found that was intermediate between two species growing in the area. In such cases, introgression was not strongly suggested.

An example of this type of hybridization is the occasional, random hybrid that occurs between *T. punctulata* Schlechtendal & Chamisso and *T. kirchoffiana* Wittmack in the highlands of northern Puebla, Mexico. These two species grow in large, sympatric populations. *Tillandsia kirchoffiana* has an elongated inflorescence with long, narrow primary bracts subtending narrow branches that about equal or slightly exceed the bracts. Internodes between adjacent branches are about half the length of the branch. Primary bracts and floral bracts are red. *Tillandsia punctulata*, on the other hand, has digitately arranged, inflated branches that are nearly as broad as they are long. Occasional specimens have simple, unbranched inflorescences. Subtending red primary bracts are approximately half the length of the branches, and the floral bracts are green. *Tillandsia punctulata* typically flowers from December through January, and *T. kirchoffiana* from January through March. Flowers in each case are lavender and about the same size. Those of *T. kirchoffiana* have green filaments and are diurnal, while nocturnal flowering *T. punctulata* features lavender filaments and white petal tips. Since flowers of *T. punctulata* remain open a full day, a single pollinator could serve both species.

Several hundred individuals of each species were examined in situ across a distance of several kilometers. Only two putative hybrids were encountered and these were separated by several kilometers. Both were approximately intermediate in morphology between the assumed parents (Fig. 1).



Fig. 1. Random hybrid *Tillandsia punctulata*, left; *Tillandsia kirchoffiana*, right; putative hybrid, center.

Pollen viability was 95% for *T. punctulata* and *T. kirchoffiana*, but only about 50% for the suspected hybrid (Table 3). The reduced pollen viability of this sample supports the notion that the specimen was of hybrid origin.

More extensive hybridization and introgression were noted in other *Tillandsia* populations where hybrid swarms of plants incorporating various combinations of characteristics of the putative parent species were encountered. In the highlands of Chiapas, Mexico, near San Cristóbal de las Casas, *T. rotundata* (L. B. Smith) C. S. Gardner appears to be hybridizing with *T. rodrigueziana* Mez. The first species has a long scape bearing a dense head of short, broad, digitately arranged branches, the floral bracts are blood-red and have the appearance of a polished surface. Branches of the second species are more widely spaced, longer, narrower and recurved. Floral bracts are yellow.

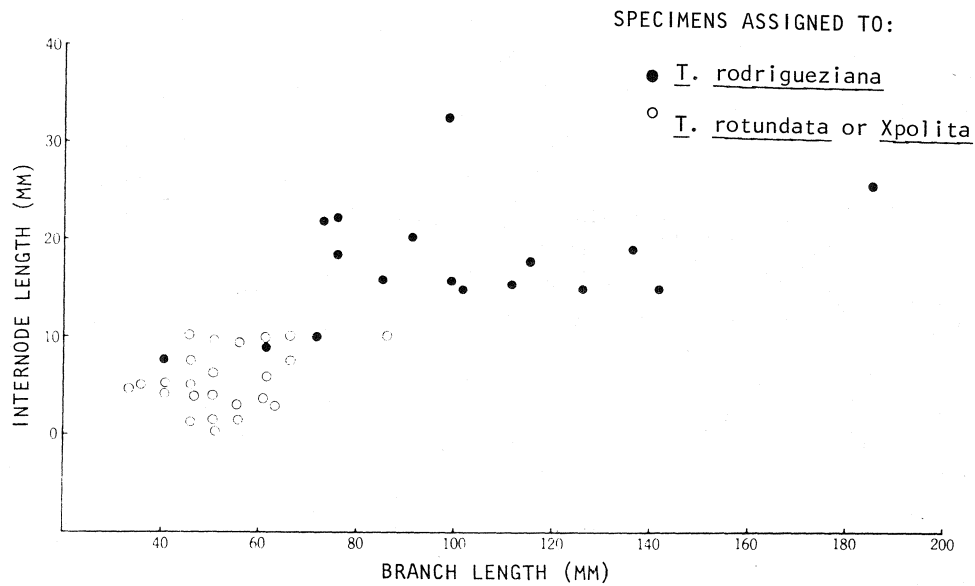


Fig. 2. Scatter diagram showing distribution of internode and branch lengths in a hybrid population involving *T. rotundata* and *T. rodrigueziana*.

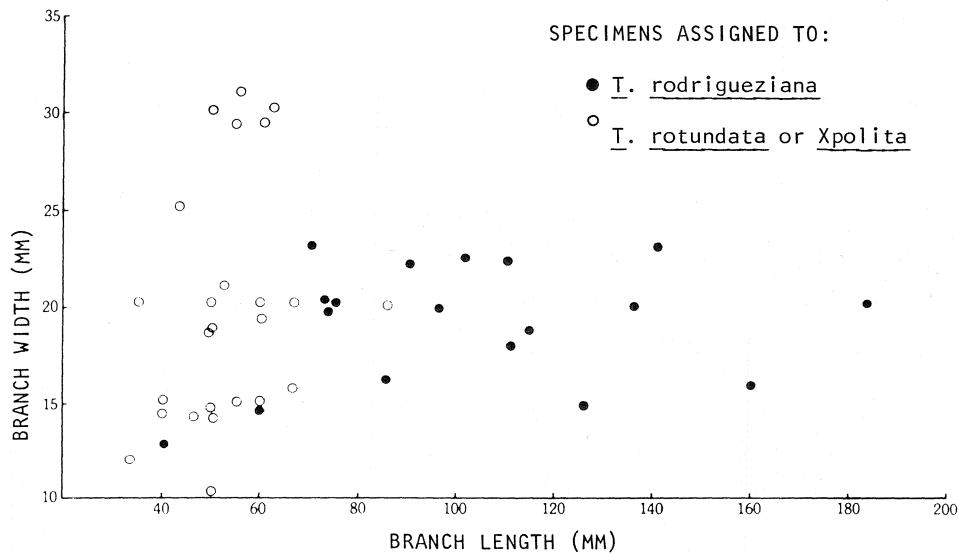


Fig. 3. Scatter diagram showing distribution of branch widths and lengths in a hybrid population involving *T. rotundata* and *T. rodrigueziana*.

Intermediate specimens collected at this site displayed a variety of morphologies combining the characteristics of the putative parents. Scatter diagrams illustrate the combinations of the characters, internode length versus branch length (Fig. 2) and branch length versus branch width (Fig. 3) among the specimens. The holotype of *T. polita* L. B. Smith, *Standley 62465* (F), which was collected in Guatemala, was compared with these specimens and matches some of the hybrid specimens well (Gardner, 1983).

A pollen sample of *T. rodrigueziana* from a different population in Chiapas, was estimated to have above 90% viability. No estimate of pollen viability was made for *T. rotundata* since all flowering material available was thought to be of hybrid origin. Pollen was examined from six putative hybrid specimens and the percentage of stainable pollen was very low — zero to 18% (Table 3). A few intermediates were found in fruit. However, attempts to produce fruit by depositing pollen of *T. fasciculata* on one to three stigmas each of these six plants did not result in fruit set. The large number of individuals in the population and their range of variation suggested that many were not primary hybrids, but were closer to *T. rotundata*. A three dimensional plot of PCA projections (Fig. 4), based on characters in Appendix 1, illustrates the phenetic relationships of a sample of these hybrids to typical individuals of the assumed parent taxa. One hybrid individual (arrow) differed from all the others by having lepidote floral and primary bracts. Hybridization with a third species may be responsible.

Another species pair from the same area that displays a pattern of morphological variation indicating hybridization is *T. seleriana* Mez and *T. butzii* Mez. *Tillandsia seleriana* has inflated leaf sheaths that form a pseudobulb, and tomentose involute blades. The inflorescence consists of a short, stout scape, stout branches separated by short internodes, and tomentose, rose-colored primary and floral bracts. Petals and filaments are lavender. After flowering, one or two offsets appear. *Tillandsia butzii* also has inflated, pseudobulbous sheaths and involute blades but the sheaths are typically less than 1/4 as large as those of the previous species and the blades are longer. Leaves are dark purple-brown and heavily marked with large, pale green, often confluent spots that tend to form irregular transverse bands. Shoot surfaces are covered with appressed scales. The inflorescence has a thin scape that is shorter than the leaves, but longer than that of *T. seleriana*, and narrow branches. Primary and floral bracts are glabrous or have sparse, minute scales and are marked like the leaves, although less distinctly. It offsets freely and forms large clumps. In the area of San Cristóbal de las Casas, many of the specimens of *T. butzii* are larger than typical with much larger pseudobulbs and offsetting is reduced to one or two per rosette. The aberrant morphology alone did not suggest hybridization. However, several individuals, approximately intermediate between the species, were found indicating the possibility that introgression from *T. seleriana* to *T. butzii* is occurring (Fig. 5). Pollen of *T. seleriana* from the population in question was stained and estimated as highly viable at 94% while pollen from *T. butzii* from the same area, not an obvious hybrid, was only 67% stained.

The members of a third species pair in Chiapas, apparently involved in introgression, were both treated as varieties of *T. fasciculata* by Smith and Downs (1977): *Tillandsia fasciculata* var. *densispica* Mez and *T. fasciculata* var. *venospica* Mez. Bertero's *T. compressa* was treated as a synonym of this variety by Smith and Downs (1977) although they noted that in Jamaica it appeared to be a distinct species. Their reluctance to recognize it as a species is because "elsewhere its characters are not stable and consequently in viewing it as a whole" they felt forced to consider it a variety. Near Ocozocoautla in a semiarid region of the central depression of Chiapas, the taxa are sympatric. *Tillandsia fasciculata* var. *densispica* has a long scape, about 1/2 to 2/3 the length of the leaves and a dense head of branches that rarely exceeds 10 cm. Floral bracts are orange-red. *Tillandsia compressa* has a much shorter scape and typically a simple inflorescence consisting of one elongated spike that usually exceeds 20 cm. Floral bracts are yellow, prominently

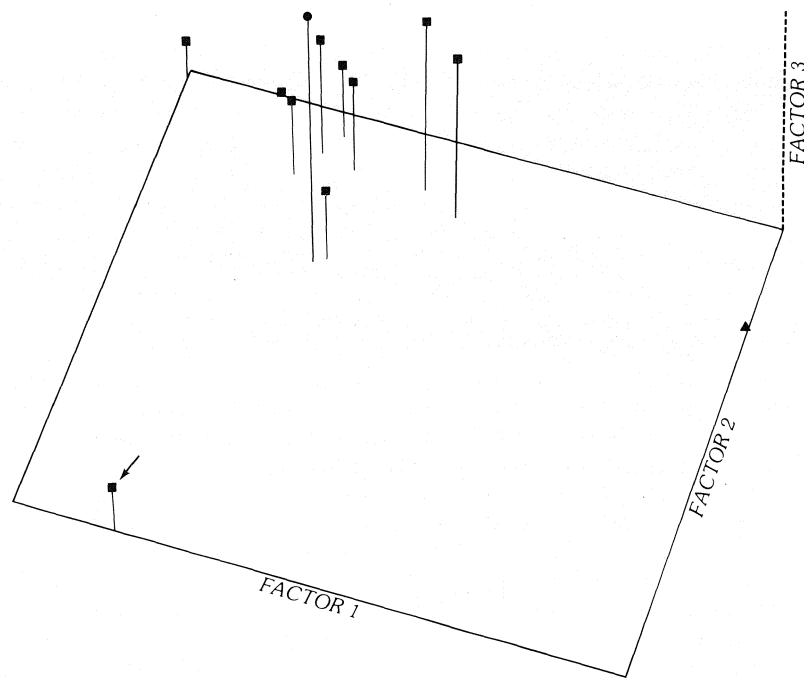


Fig. 4. PCA plot illustrating phenetic relationships among specimens from a hybrid population and the putative parental species. *T. rotundata* (from another population), circle; *T. rodrigueziana* (from another population), triangle; specimens from area of hybridization, squares.



Fig. 5. Introgressive hybrids. *Tillandsia butzii*, left; *Tillandsia seleriana*, right; putative hybrids between.

beaked, and nearly 1/3 larger than those of the previous taxon. At this study site, *T. compressa* flowers May to July, and *T. fasciculata* var. *densispica* July to August. Smith and Downs (1977) also noted that Proctor reported the two species have distinct flowering seasons in Jamaica. Most individuals examined near Ocozocoautla were easily assigned to one species or the other. However, a few individuals were intermediate, and occasional *T. compressa* specimens had branched inflorescences. A pollen sample from a typical *T. compressa* was mostly viable (95%), while that of a specimen with a branched inflorescence was only 40% stained suggesting that hybridization could be a factor in its branching. The intermediates which caused Smith and Downs to treat these taxa as varieties of a single species could have been hybrids.

Two populations of *T. utriculata* are suspected of interspecific hybridization. One is located near Cardenas, San Luis Potosi, Mexico, where it is sympatric with *T. limbata* Schlechtendal. Intermediates were common. The species typically occupy parallel geographic distributions, but they are separated by different climatic requirements and often occur only a few kilometers apart. *Tillandsia utriculata* has a primarily coastal distribution where it occupies highly exposed sites as an epiphyte in thinly developed canopies, or on exposed rock surfaces in areas characterized by low rainfall and high humidity. *Tillandsia limbata* occurs in denser tree crowns of wetter regions. The site near Cardenas is relatively dense, moist forest, but much of it has been cleared or thinned. The two species are similar in most of their morphological characters. *Tillandsia limbata* has a pinnate inflorescence with strongly distichous and geniculate branches. *Tillandsia utriculata*'s inflorescence is often bi- or tripinnate, branches are flexuose, and while they tend to be distichous, they are not strongly so. Floral bracts of *T. limbata* are broad, glabrous and smooth when fresh or dry, cover the sepals and envelop the rachis. Those of *T. utriculata* are smaller than the sepals, do not cover any of the rachis, are often sparsely lepidote and are slightly to moderately nerved when dry. The putative hybrids were approximately intermediate. A few typical *T. utriculata* were found in the same host trees as were some almost typical *T. limbata*. These two species also differ in several floral characters, but flowers of the putative hybrids were not seen. Principal component analysis was used to assess the phenetic relationships among a sample of specimens from this site, and samples of the putative parents from other populations where hybridization was not suspected. A three-dimensional plot of the PCA projections (Fig. 6), based on characters in Appendix 2, illustrates their phenetic relationships. Some of the specimens from the hybrid area cluster with one parent or the other while others occupy intermediate positions.

A similar mixed situation was found in a dry forest near Tuxtla Gutierrez, Chiapas, where individual plants tend to vary from rather typical *T. utriculata* to specimens that had some resemblance to *T. makoyana* J. G. Baker — a species that occurs in the area. This species varies in several vegetative characteristics between and within populations, but the specimens share the following characters that distinguish them from *T. utriculata*: 1. branches are heavier, geniculate, and strongly distichous; 2. inflorescence branching tends to be once pinnate; and 3. foliage is rigid and nerved. This species was distinguished from *T. dasylirifolia* J. G. Baker by Smith and Downs (1977) by more strongly nerved floral bracts and less strongly geniculate rachis. Populations of the taxa intergrade in the wild. A population sample of *T. makoyana* was not available so specimens from several populations, some of which would be considered *T. dasylirifolia* by Smith and Downs, were used.

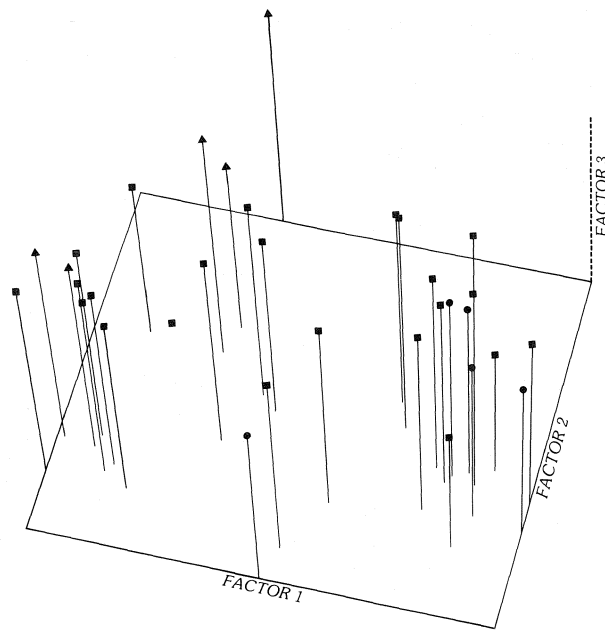


Fig. 6. PCA plot illustrating phenetic relationships among specimens from a hybrid population and the putative parental species. *T. utriculata* (from another population), triangles; *T. limbata* (from another population), circles; specimens from area of hybridization, squares.

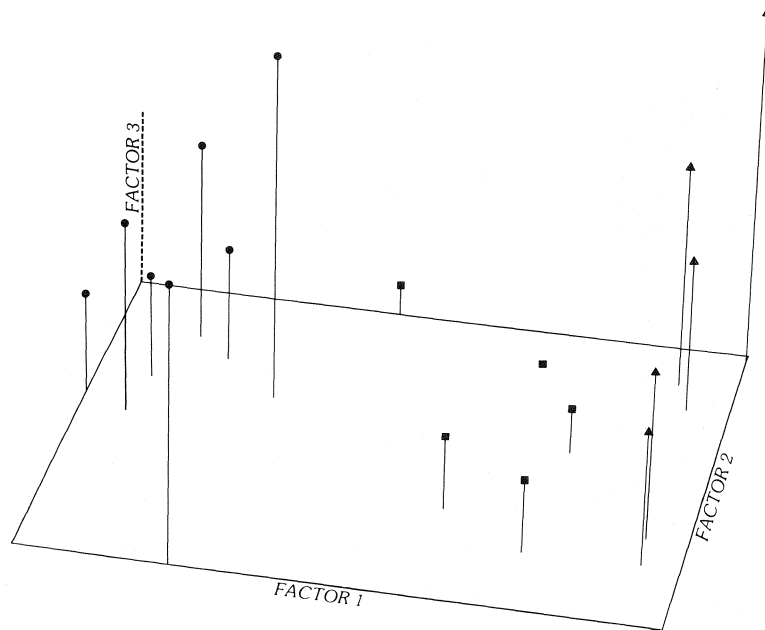


Fig. 7. PCA plot illustrating phenetic relationships among specimens from a hybrid population and the putative parental species. *T. utriculata* (from another population), circles; *T. makoyana* and *T. dasyliriifolia* (from several other populations), triangles; specimens from area of hybridization, squares.

Principal component analysis with characters in Appendix 2 were again employed to examine and illustrate the phenetic relationships among these hybrids and parental types. (Fig. 7).

No pollen from suspected *T. utriculata* hybrids was available. Fertility, however, is apparently high in the last example as the number of fruits produced, and the number of seeds per fruit from samples examined were higher than samples from several other *T. utriculata* populations (Gardner, unpublished data).

DISCUSSION AND CONCLUSIONS

Natural hybridization is fairly common among sympatric species where ecological conditions permit (Grant, 1971), and may be important in enriching gene pools (Stebbins, 1977). Sterility of hybrid offspring is a restriction that hybrid populations must overcome, but "the great success of hybrid swarms of flowering plants in colonizing new habitats has now been demonstrated by a large number of examples . . ." (Stebbins, 1977). Even rare backcrosses may have important consequences for the evolution of the species involved. It has been recognized that even a small amount of fertility can be highly significant, evolutionarily, by allowing a few genes of one species to become established in the genetic complement of another, increasing its genetic variability (Anderson, 1953).

Environmental disturbances make new niches that are often more suitable to hybrids of the surrounding plant populations than to the original species (Stebbins, 1977). Modified environments that result from human activities or other catastrophic events are often sites favored by hybrid swarms. In Mexico there are few areas that have not been affected by human activities to a greater or lesser extent. Man's influence has been widely imposed on the environment by: grazing of domestic animals; partial cutting of the forests for lumber, firewood, etc.; clearing of all native vegetation for modern agriculture; and Mayan swidden agricultural practices of "slash and burn" for temporary agricultural plots. Although the present high degree of man's modification of the environment in Latin America is fairly recent, the vegetation in these areas has been significantly disturbed for thousands of years. Mayan agriculture has been practiced for an estimated 4,500 years (Stuart and Stuart, 1977) in an area that includes most of Mesoamerica, and which extends northward to the isthmus of Tehuantepec.

Further studies using biochemical and cytological techniques may give more insight into the possible role of hybridization in the evolution of *Tillandsia* and its allies. Hybrids of *Tillandsia* may result in enriched gene pools and partially account for the wide adaptability of many species of the genus as well as for the success of the group as a whole. Regardless of the adaptive or evolutionary consequences of hybridization, its recognition as a factor in the morphological diversity of this group is essential for a better understanding of the patterns of variation and the relationships among the species.

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





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














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APPENDIX 1

Characters used for *T. rotundata* X *T. rodrigueziana*
and putative hybrids for Principal Component Analysis.

59 Characters From Exsiccate

Leaf Length (including sheath)	cm
Leaf Width (at union with blade)	mm
Sheath length	cm
Sheath width	mm
Sheath color (adaxial)	1-concolorous 2-brown 3-purple
Sheath color (abaxial)	1-concolorous 2-brown 3-purple
Sheath scales (adaxial)	1-glabrous 2-lepidote 3-densely lepidote
Sheath scales (abaxial)	1-glabrous 2-lepidote 3-densely lepidote
Distinct scales on edge of sheath	1-yes 2-no
Sheath shape	1-strongly inflated 2-weakly inflated 3-distinct 4-indistinct 5-reduced
Sheath substance	1-membranous 2-same as leaf 3-thicker than leaf
Leaf shape	1-  2-  3-  4-  5- 
Leaf cross section	1-  2-  3-  4-  5-  6- 
Leaves nerved? (dry)	1-no 2-weakly 3-strongly
Leaf substance	1-thin/soft 2-moderately thin 3-firm 4-hard
Leaf surface (adaxial)	1-glabrous 2-sparsely lepidote 3-lepidote 4-tomentose 5-extremely tomentose
Leaf surface (abaxial)	1-glabrous 2-sparsely lepidote 3-lepidote 4-tomentose 5-extremely tomentose
Scape bract lamina (upper)	1-none 2-very short 3-shorter/leaves 4-equaling leaves

- Scape bract lamina (lower) 1-none 2-very short 3-shorter/leaves
4-equaling leaves
- Scape bract (posture of lamina) 1-  2-  3- 
- Primary bracts laminate? (mid) 1-no 2-short 3-long 4-very long
- primary bracts sheath/spike (low) 1-much smaller 2-equal
3-larger 4-much larger
- Primary bract substance 1-thin 2-moderately thin 3-firm 4-hard
- Primary bract sheath surface (adaxial) 1-glabrous 2-lepidote
3-densely lepidote
- Primary bract sheath surface (abaxial) 1-glabrous 3-lepidote
3-densely lepidote
- Primary bract lamina posture 0-none 1-straight 2-arched 3-reflexed
- Number of flowers/branch 1-one 2-(2-4) 3-(5-8) 4-(9-15) 5-more
- Secondary branching (where?) 1-none 2-lower only 3-all
- Inflorescence pinnate (maximum) 0-none 1-once 2-twice 3-thrice
- Branch posture 1-terminal 2-  3-  4- 
- Branch curvature 1-  2-  3-  4- 
- Sterile bracts keeled? 0-none 1-no 2-yes 3-2 keels
- Sterile bract number
- Branch pedicle (length naked) 1-none 2-short 3-moderate 4-long
- Internode between branches 1-none visible
2-1/4 length of branch or less 3-1/2 to equal length of branch
- Floral bract/internode 0-none 1-more/2X 2-2X or less
3-equal 4-shorter 5-much shorter
- Floral bract length mm
- Floral bract width mm
- Floral bract cross section 1-  2-  3-  4- 
- Floral bract apex 1-  2-  3-  4-  5- 
- Floral bracts nerved? 1-no 2-edges only 3-weakly
- Floral bract substance 1-membranous 2-thin 3-medium
4-coriaceous 5-hard
- Floral bract sinus at midbase 1-no 2-weak 3-strong
- Floral bract surface (adaxial) 1-slick 2-glabrous
3-sparsely lepidote 4-lepidote
- Floral bract surface (abaxial) 1-slick 2-glabrous
3-sparsely lepidote 4-lepidote
- Sepal length mm
- Sepal width mm
- Sepals connate? 1-none 2-posterior only 3-all
- Posterior sepals connate? 1-no 2-weakly 3-1/3 4-1/2 5-more
- Sepals carinate? 1-no 2-posterior only 3-all
- Posterior sepals carinate? 1-no 2-weakly 3-moderately
4-strongly 5-very strongly

Sepals nerved? 1-no 2-slightly 3-moderately 4-strongly
 Sepal apex 1-  2-  3-  4- 
 Sepal shape 1-broad base 2-broad middle 3-broad apex
 Sepals all alike? 1-alike 2-similar 3-different
 Sepal surface (adaxial) 1-glabrous 2-sparsely lepidote 3-lepidote
 Sepal surface (abaxial) 1-glabrous 2-sparsely lepidote 3-lepidote
 Sepal scales distribution (abaxial) 1-none 2-evenly distributed
 3-concentrated on apex 4-concentrated on edges
 Sepal substance 1-membranous 2-thin 3-medium 4-firm 5-hard

APPENDIX 2

Characters used for *T. utriculata* and putative hybrids
 for Principal Component Analysis

21 Characters From Exsiccate and Field Notes

Height cm
 Substrate 1-cacti/yucca 2-woody shrubs 3-thorn trees 4-oaks
 5-other hardwood 6-pines 7-rocks
 Leaf length cm
 Leaf-blade width mm
 Leaf-sheath width mm
 Leaf-blade shape 1-triangular 2-intermediate 3-acuminate
 Inflorescence compounding 1-simple 2-bipinnate 3-tripinnate
 Caulescence 1-caulescent 2-acaulescent
 Angle of rachis angle of bend at flower insertion
 Flower disposition 1-strongly distichous 2-subdistichous
 3-polystichous
 Floral bract length mm
 Floral bract width mm
 Floral bract substance 1-coriaceous 2-membranous edge
 3-membranous
 Floral bract surface (abaxial) 1-glabrous 2-sparse trichomes 3-scurfy
 Floral bract nerved? 1-strongly/evenly 2-moderately 3-faintly
 4-edges only 5-not nerved
 Sepal length mm
 Sepal width mm
 Sepal union 1-free 2-slightly connate 3-1/2 connate or more
 Sepal substance 1-coriaceous 2-membranous edge 3-membranous
 Trichome diameter .001 mm
 Clonality 1-no offsets 2-small basal offsets 3-leaf axial offsets